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MORPHOLOGY, PHYLOGENY, AND BEHAVIOR OF *ANOLIS PROBOSCIS*

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ABSTRACT. Males of the three species of the *Anolis laevis* group, so-called proboscis anoles, display a remarkable appendage extending from the snout. All *A. laevis* group *Anolis* are poorly known and rarely collected. We redescribe *Anolis proboscis* based on the type specimen and male and female specimens we collected recently near the town of Mindo, Pichincha Province, Ecuador. We include color notes and additional morphological measures lacking from the original description, natural history data for 11 specimens, an estimate of the phylogenetic relationships of the species, and a description of display behavior and intraspecific interactions incorporating the proboscis.

KEY WORDS: *Anolis proboscis*; Ecuador; redescription, behavior

Among the myriad strange and varied *Anolis*, from semiaquatic forms such as *A. barkeri* to a blue insular species *A. gorgonae* to a colorful dewlapless cliff dweller *A. bartschi*, the three species of proboscis anoles with their scaly anterior snout extensions stand out as especially curious. Originally described from few specimens and no females (*Scytomycterus* [*Anolis*] *laevis* Cope 1876, n = 1; *A. phyllorhinus* Myers and Carvalho 1945, n = 2; *A. proboscis* Peters and Orces-V 1956, n = 6) and for many decades unreported in life since their descriptions, two of the three species of proboscis anoles have recently been rediscovered. Rodrigues *et al.* (2002) described the first female proboscis anoles of *A. phyllorhinus* from Amazonia. Almendáriz and Vogt (2007) reported on a male *A. proboscis* captured but released near Mindo, Ecuador, and Yánez-Muñoz *et al.* (2010) described variation in five specimens of *A. proboscis*.

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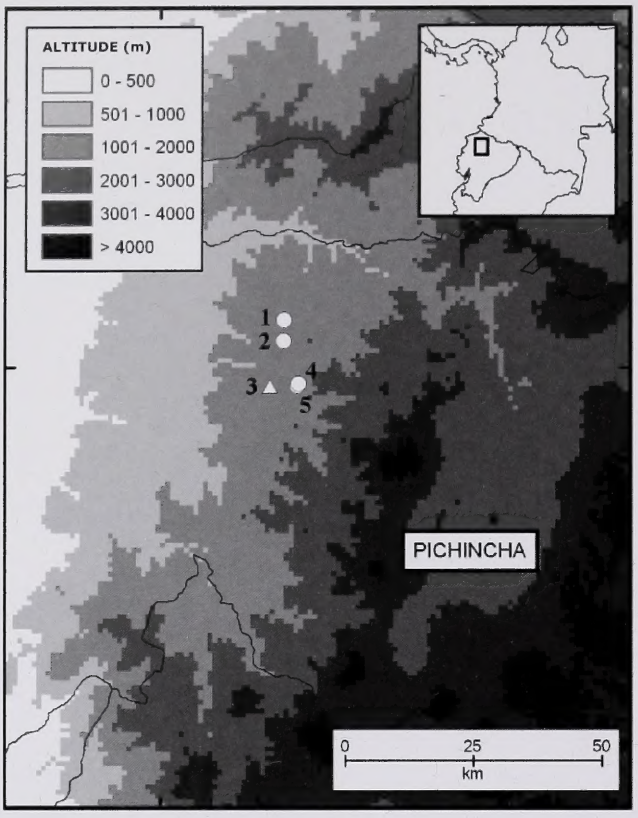

Figure 1. Collecting localities for *Anolis proboscis* near Mindo, Pichincha Province, Ecuador (latitude, longitude, elevation in parentheses): (1) Tulipe (0°4′58.8″N, −78°46′58.8″W) (2) Las Tolas (0°2′45.5994″N, −78°47′5.9994″W), (3) Cunuco, 5 km NW Mindo (−0°1′58.8″S, −78°48′28.8″W), (4) 5 km E Mindo (−0°1′55.2″S, −78°45′36″W), (5) turnoff to Mindo, 1–5 km down from intersection (−0°1′55.2″S, −78°45′36″W).

The paucity of specimens of *A. laevis* and *A. phyllorhinus* in museum collections may be explained by the remote ranges of these species. The single specimen of *A. laevis* is from a mountain trail connecting two lower elevation Peruvian towns, and *A. phyllorhinus* is an Amazonian forest form with an apparently small distribution. The rarity of *A. proboscis* in collections is more surprising. The type locality of this species is a populated area within 3 hours drive of Quito along a well-traveled, paved road. The area in which the species has been found is a famous birding site with several hotels frequented by ecotourist groups and scientists alike.

In August 2009, a joint expedition of the University of New Mexico and the Pontificia Universidad Católica del Ecuador, Quito collected three males and two females of *A. proboscis* in approximately 8 hours of searching along the paved road leading from the major western Ecuadorean Highway, Vía Calacalí–Los Bancos, to Mindo (Fig. 1). This locality is within 5 km of Cunuco, the type locality of *A. proboscis*. A second expedition in December 2009 found six specimens of *A. proboscis* in approximately 2 hours of searching at the same locality.

The type specimen of *A. proboscis* was well described by Peters and Orces-V. (1956), but the description lacked information on some standard characters in *Anolis*, such as number of scales across the snout between the second canthals (a common measure of head scale size). Williams (1979) reviewed the proboscis anoles but had no information on them in life. Yánez-Muñoz *et al.* (2010) described external variation in their newly collected material but did not report on osteology, redescribe the type specimen, or compare their material to previously collected specimens. Here we present a redescription of the holotype of *A. proboscis* (MCZ 54300); describe variation in newly collected and previously preserved specimens of the species, including characters not previously scored in *A. proboscis,* such as toe length, size of ventral and dorsal body scales, and skull structure; perform a phylogenetic analysis to determine the placement of this species within *Anolis*; and present data on the color, behavior, and ecology of *A. proboscis* in life.

MATERIALS AND METHODS

Measurements were made with digital calipers on preserved specimens and are given in millimeters (mm), usually to the nearest 0.1 mm. Snout to vent length (SVL) was measured from the anterior tip of the lower jaw to the anterior margin of the cloaca. Head

length was measured from the tip of the snout to the anterior edge of the ear. Femoral length was measured from the midline of the venter to the knee, with the knee bent at a 90° angle. Head width was measured at the broadest part of the head between the posterolateral corners of the orbits. Tail length was measured from the anterior margin of the cloaca to the tip of the tail. Toe length was measured from the origin of the fourth (i.e., longest) toe to the tip of its claw. Scale terminology and characters used mainly follow standards estabflished by Williams (e.g., Williams *et al.*, 1995) for species descriptions of *Anolis* lizards. Skull description is given in terms of Etheridge's (1959) and Poe's (1998, 2004) characters. See those papers for more detailed descriptions of skull conditions and alternative conditions in *Anolis*.

For phylogenetic analysis, we added 59 species to the dataset of Poe (2004), which included *A. proboscis*. Species were added to obtain a better estimate of the closest relatives of *A. proboscis* because many potential sister species for *A. proboscis* were not included by Poe (2004).

We generated a novel phylogenetic estimate of *A. proboscis* using a dataset of 91 morphological characters (Poe, 2004; unpublished morphological data for 57 additional species), 979 sites of mtDNA (NADH dehydrogenase subunit 2, five transfer RNAs; Nicholson *et al.*, 2005), and 1,179 sites of nuclear DNA (internal transcribed tracer region; Nicholson 2002) for 265 species of *Anolis* and eight outgroups. Data coverage varied from all 1,267 parsimony-informative characters scored to 52 parsimony-informative characters for some species scored only for external morphology. The matrix includes large amounts of missing data; for 75 species, only varying amounts of morphological data were scored.

We used a partitioned Bayesian analysis with separate GTR + gamma models for the two DNA data sets and the "standard" model for the morphological data with "informative" coding and "ordered" and "unordered" coding for characters according to Poe (2004). Topology was assumed to be shared between each of the three partitions, whereas branch lengths were allowed to vary. We ran two independent analyses for 10 million generations, sampling every 500 generations, resulting in 20,001 trees. For each analysis, we ran three heated and one cold chain with heating temperature = 0.1. We checked for convergence by monitoring the standard deviation of split frequencies and the natural log likelihoods of each sampled generation. We discarded the first 19,000 trees as burn-in, leaving 1,001 trees for analysis.

We also performed a parsimony analysis in PAUP* (Swofford, 2002) with all characters weighted equally. We used the parsimony ratchet (150–200 repetitions, 10–35% character removal; Nixon, 1999) to find an optimal tree and then swapped on this tree using the tree-bisection-reconnection search in PAUP*. Support for individual clades was evaluated using the bootstrap (Felsenstein, 1985). For bootstrap analysis, 100 replicate matrices of the same size as the original were constructed by sampling characters with replacement. Replicate matrices were analyzed with parsimony using one round of random taxon addition and TBR branch swapping with a time limit of 600 seconds per rep. Resulting trees were summarized by mapping bootstrap values greater than 50% onto the optimal parsimony tree.

REDESCRIPTION OF *A. PROBOSCIS*

Anolis proboscis Peters and Orces-V. 1956
Figures 2–3

Holotype. MCZ 54300, adult male, Ecuador, Cunuco, 5 km NW of Mindo, 27–29 April 1953, Antonio Proaño collector.

Additional Material. USNM 207671, adult male, Ecuador, vicinity of Mindo, date of

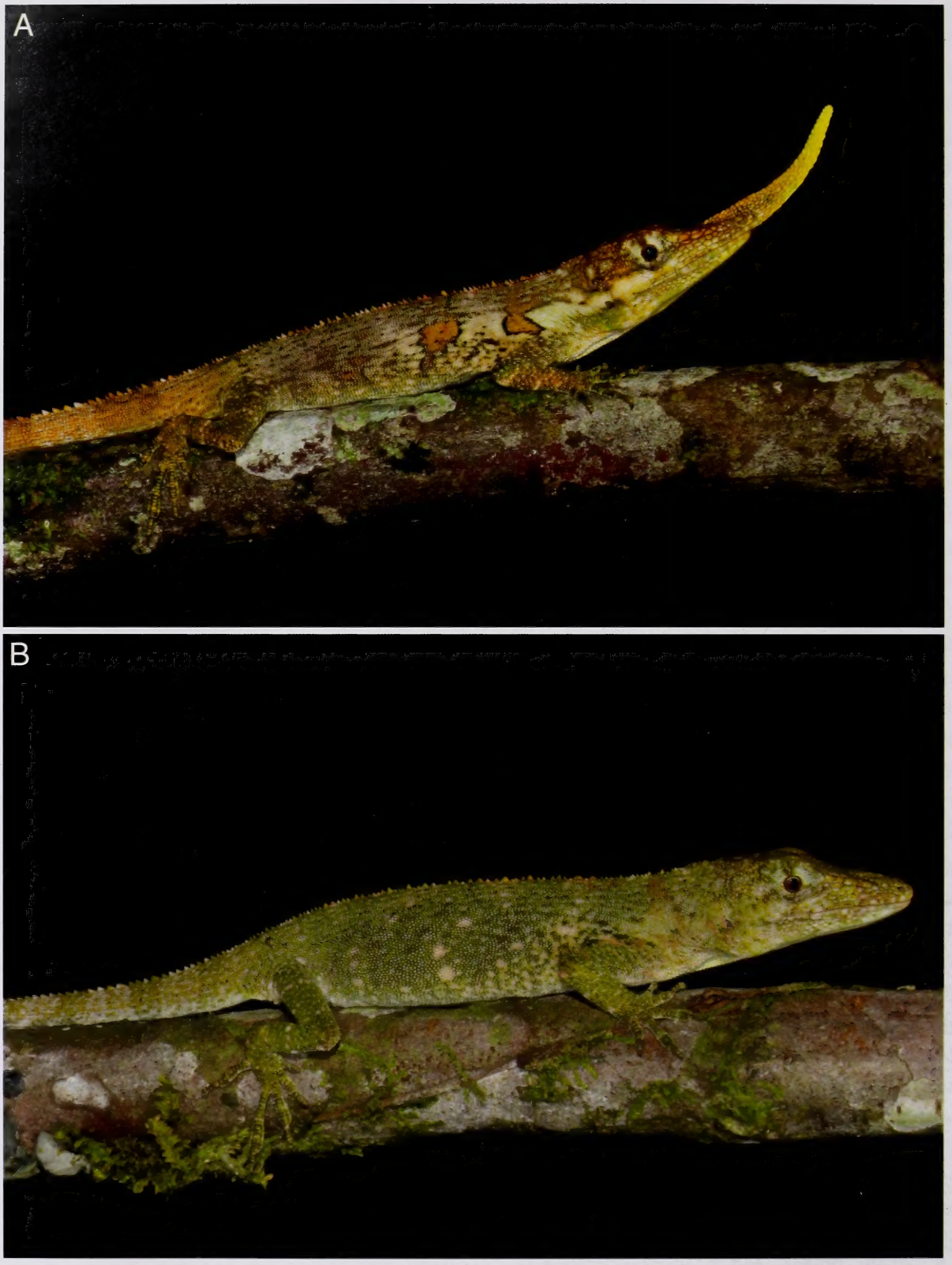

Figure 2. *Anolis proboscis* collected near Mindo, Ecuador. A, male; B, female.

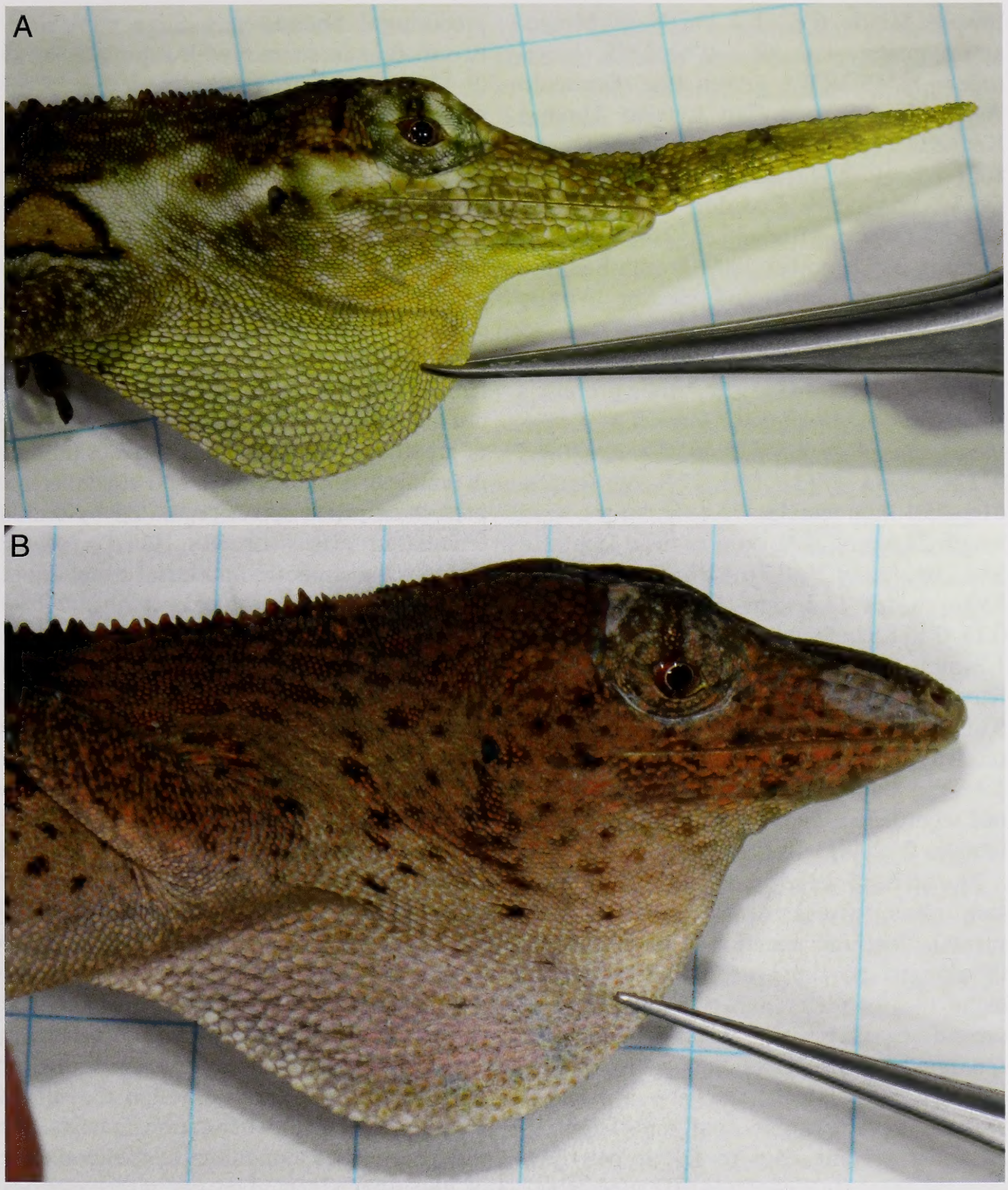

Figure 3. Dewlap of *Anolis proboscis*. A, male; B, female.

collection unknown, Rosero collector; USNM 207672–3, adult males, Ecuador, vicinity of Mindo, August 1964, M. Olalla collector; QCAZ 9717, adult male, 5 August 2009; QCAZ 9718 adult female, 5 August 2009; QCAZ 9734–35 adult males, 7 August 2009; QCAZ 9753, adult female, 10 August 2009; Ecuador, 1–4 km from turnoff

toward Mindo (i.e., 2–5 km N of Mindo; approximately latitude −0°1′58.8″S, longitude −78°45′36″W); Steven Poe, Fernando Ayala, Eric Schaad, Ian Latella, Thomas Kennedy, Natalie Blea collectors; QCAZ 8061–63, 10209–11, same locality as other QCAZ specimens; Ecuador, 1–4 km from turnoff toward Mindo (i.e., 2–5 km N of Mindo), 28 December 2009, Steven Poe, Ian Latella, Levi Gray, and Beeling Armijo collectors.

Description of External Morphology of the Holotype (MCZ 54300) of Anolis proboscis *(Variation in Additional Material in Parentheses, Based on USNM 207671–3, QCAZ 9717–8, 9735, 9753).* SVL 72.9 mm (males: 61.1–75.1 mm; females: 70.4–72.6 mm); head length 22.3 mm, 0.31 ratio of head length to SVL (males: 0.26–0.31 SVL; females 0.26 SVL), width 11.1 mm, 0.15 SVL (males: 0.14–0.15 SVL; females 0.14 SVL); ear height 1.3 mm, 0.01 SVL (males: 0.01–0.02 SVL; females: 0.02); femoral length 14.4 mm, 0.20 SVL (males 0.20–0.22 SVL; females 0.21); tail length not recorded in Type (males 1.1–1.4 SVL; females 1.3 SVL); fourth toe length not recorded in Type (males 0.13–0.14 SVL, females 0.12–0.13 SVL).

Dorsal head scales smooth; frontal depression absent (weak); rostral extends over mental, reaching anterior triangular peak inferior to proximal aspect of proboscis; eight (8–10) scales across snout between second canthals; supraorbital semicircles separated by two scales; suboculars in contact with supralabials; elongate supraciliary scales not evident, only small undifferentiated scales present; four to five loreal rows; circular nasal scale contacts first supralabial, separated from rostral by two scales; interparietal length 2.6 mm (0.04 SVL; 0.03–0.04); ratio of length of interparietal to length of second largest scale lateral to interparietal 3.7 (2.1–2.4); two scales separate interparietal and supraorbital semicircles; preoccipital absent; very large sublabials, two to four in contact with supralabials; 10 (9–12) supralabials to center of eye; 8–13 postrostrals; four (3–4) postmentals; some slightly enlarged scales present in supraocular disc, decreasing gradually in size; mental partially divided posteriorly, extending posterolaterally beyond rostral, with posterior border in concave arc (or concave); five (2–6) greatly enlarged sublabials, three (2–3) in contact with infralabials; dewlap reaches just posterior to axillae (same in males and females); scales on dewlap closely packed, not in regular rows; no axillary pocket; a pair of greatly enlarged postcloacal scales (absent in females); nuchal, dorsal, and caudal crests present as raised spikes separated by undifferentiated scales (Lazell's [1969] type 5); dorsal scales smooth; middorsal scales equal in size to lateral scales (except crest), 10 (9–11) longitudinal rows in 5% of SVL; ventral scales in transverse rows, smooth, nine (6–9) scales in 5% of SVL; limb and supradigital scales smooth; toepads expanded; 19 (20–22) expanded lamellae under fourth toe.

The proboscis (Fig. 2A; absent in females) is a laterally compressed, pliable appendage covered with somewhat elongate scales that are slightly smaller than the dorsal headscales. The posterior aspect of the proboscis rises longitudinally from the midsnout region and extends forward with a partially serrated dorsal edge, eventually coming to a blunt anterior end. Neither the rostral nor the supralabials form significant parts of the proboscis, although the supralabial/loreal scale demarcation extends anteriorly as a line along the ventrolateral edge of the appendage. The proboscis extends anteriorly 85% of the head length beyond the snout (mean 77–89.5% for three adult males; 62% for one juvenile male of SVL 53 mm; Table 1).

Skull Description (Based on Dry Skeletons USNM 207673, QCAZ 9734). Parietal roof

TABLE 1. MEASUREMENTS OF SPECIMENS OF *ANOLIS PROBOSCIS* SHOWING LENGTH OF PROBOSCIS RELATIVE TO SNOUT TO VENT LENGTH (SVL) AND HEAD LENGTH. MEASUREMENTS ARE IN MILLIMETERS.

Specimen	SVL	Head Length	Proboscis Length
QCAZ 9717	59.9	16.9	13.9
QCAZ 9734	NA	19.7	17.6
QCAZ 9735	69.3	19.4	15.0
QCAZ 8061	53.4	16.4	10.1
QCAZ 8063	73.1	22.8	19.6

Note: Snout to vent length for specimen QCAZ 9734 was unavailable because the body of the specimen was not intact.

flat, with convex V- or Y-shaped crests, with slight casquing, lacking crenulation on edges, extending slightly posteriorly over supraoccipital; anterolateral corners flush with posterolateral edges of frontal; pineal foramen at parietal-frontal suture; dorsal skull bones smooth; postfrontal present; prefrontal contacts nasal between frontal and maxilla; frontal sutures anteriorly with nasals; no parallel crests on nasals; external nares bordered posteriorly by nasals; dorsal aspect of jugal terminates on lateral surface of postorbital; jugal contacts squamosal; posterodorsal ramus of squamosal long, may contact parietal above supratemporal; posterior aspect of jugal mostly straight; epipterygoid short, does not contact parietal dorsally; pterygoid and palatine teeth absent; lateral edge of vomer smooth, without posteriorly directed lateral processes; maxilla extends posteriorly beyond ectopterygoid on ventral surface of skull; crest between basipterygoid processes of basisphenoid absent; lateral shelf of quadrate absent; some black pigment on the dorsal surface of parietal and frontal; nasals overlap premaxilla dorsally or are flush with it; dorsal surface of supraoccipital with single central process; posteriormost mandibular tooth partially anterior to anterior mylohyoid foramen; large splenial present; ventral aspect of anteromedial process of coronoid extends posteriorly; labial process of coronoid present; external opening of surangular foramen is entirely within surangular; posterior suture of dentary is pronged; anteriormost aspect of posterior border of dentary anterior to mandibular fossa; jaw sculpturing absent; angular absent; angular process of articular present, small.

Color in Life (Adapted from Field Notes). Below we describe two color morphs each in males and females. QCAZ 9717 (male; Fig. 2A): dorsum white laterally with three broad peach blotches outlined with black (one above axilla, two around midbody); middorsum green becoming orangeish at pelvis, with orange extending back onto tail; top of head brown, lacking interorbital bar; white from under eye back to body; peach blotch above axilla; limbs mottled rust and green; belly white with brown; tail strongly banded; dewlap white with white scales, with some scales faint yellow-green or peach (Fig. 3A); throat off-white; tongue tan; iris brown; eyelids white; scales on proboscis orange-brown.

In the second male morph (QCAZ 9734), the lateral blotches (midbody and axillary) are entirely black rather than peach with black edges. In at least one specimen (QCAZ 9735), the proboscis is greenish yellow anteriorly.

QCAZ 9718 (female) dorsum brown, almost no green, largely patternless but somewhat mottled with lighter brown, black, and peach; top of head orange-brown, peach-brown laterally; belly cream with peach tint; tail faintly banded; iris brown; dewlap skin white, scales white to peach (Fig. 3B).

The larger female (QCAZ 9753; Fig. 2B) was recorded as more greenish-brown than QCAZ 9718.

Neither males nor females exhibited much color change while alive beyond slight darkening and lightening.

Ecology, Behavior, and Habitat. The 6.3-km spur road connecting Mindo to the Vía Calacalí–Los Bancos Highway descends steeply through pasture and good patches of secondary forest from an altitude of 1,679 m at the highway to 1,275 m at the bridge, signaling the entrance to Mindo. Despite at least equal effort in other areas around Mindo, including some with better forest at similar elevations, all of our specimens of *A. proboscis* were collected along this road. *Anolis gemmosus, A. fraseri,* and *A. aequatorialis* are sympatric with *A. proboscis* here. We found perhaps 50 individuals of *A. gemmosus* per *A. proboscis* record, with most of these on ferns less than 3 m above the ground. *Anolis aequatorialis* was less abundant than *A. gemmosus,* but still common, and was extremely abundant in nearby forest. We found only two *A. fraseri* along the road to Mindo but collected several specimens of this species at a slightly lower elevation along the Río Mindo just northwest of town.

All 11 of our specimens of *A. proboscis* were collected sleeping at night horizontally on twigs, except QCAZ 8061. QCAZ 8061 is a juvenile male that was found sleeping in a vertical position on the twig of a tall tree 3 m above ground in steep, highly disturbed terrain in a grove of sparsely vegetated trees by the road. QCAZ 9717 was 3.5 m aboveground in a tangle of bare twigs below a dense higher canopy in a patch of good forest. QCAZ 9718 was 8 m aboveground on a bare twig in a disturbed area adjacent to good forest. QCAZ 9734 was approximately 9 m above the side of a ravine (approximately a meter above eye level from the edge of the ravine) on a bare twig in a disturbed area. QCAZ 9735 was 4 m aboveground on a leafy twig in a highly disturbed area of pasture with isolated brush and small trees. QCAZ 9753 was 6 m aboveground on a leafy twig in the same area.

The sleeping behaviors of QCAZ 8062–63, 10209–11 were recorded as follows. Two specimens (male and female) were collected approximately 8 m aboveground, within 2.5 m of each other in a sparsely vegetated tree on the edge of good forest by the road. Two specimens were collected on twigs of small (~ 4 m) trees at 2 and 2.5 m height, respectively, along the road bordering pasture. One adult female was 3.5 m aboveground on a bare twig in pasture approximately 30 m from the road.

The sleeping posture of *A. proboscis* is reminiscent of twig anoles of the Caribbean (Thomas, 1965) and *Phenacosaurus* anoles of South America. Captive behavior suggests the tail is prehensile, as specimens periodically wrapped the tail around twigs.

Subsequent to our visits to where the species was initially collected, one of us (J.C.) was able to observe the behavior of *A. proboscis* in life. He provided the following notes:

> "I had an opportunity to photograph a full courtship to copulation sequence, but things proceeded so quickly that I was left only with a few shots of the copulating pair. Notwithstanding, I was at least able to observe the employment of the proboscis in the courtship display. Predictably, before closing the distance the male dewlap displayed, followed by a rush toward the female, during which the proboscis was flourished quickly from side to side in several stereotyped, rather 'mechanical looking' sweeps of the head. The male then elevated the proboscis to 45 degrees and then appeared to seize the female by the nape in typical *Anolis* fashion (my view was partially obstructed at times). The male moved very rapidly and aggressively throughout, and copulation occurred within seconds of the initiation of courtship behavior, in contrast to the much lighter touch that I have observed in, for example, *A. gemmosus*."

"Having in my possession two males of similar size, I decided to place them together on a branch and attempt to record any resulting behavior. To my surprise the individual that had seemed more robust, and that had fed more freely in captivity, immediately deferred to a male that appeared slighter of build. The submissive male flattened himself against the limb, adopted a dark brown coloration, and remained immobile while being threatened by the other. The aggressor assumed bright colours, laterally compressed its body, gaped, flared its dewlap while bobbing its head slowly, and approached very deliberately, with proboscis arrow straight. As the dominant male neared the submissive one it pointed its head downward at a shallow angle and brought its proboscis parallel with the head of the other male, sometimes touching it lightly. It maintained this stance until the submissive male broke and ran. When these two animals were released together at the capture site, hours later, the submissive male remained terrified of the other and climbed rapidly away from it."

"A male, some time after being removed from its terrarium and placed on branches, spontaneously dewlap displayed while scanning its surroundings. I never observed any apparent use of the proboscis as a long-range signal."

"Captive animals fed readily on small Acrididae. A male fed on a small caterpillar and a leaf beetle while at liberty during a photo shoot. A female, released at its capture site, attacked and began to consume a polydesmid millipede within minutes of being set free. Males elevated the proboscis to roughly 45 degrees when stalking and seizing prey."

Relationships. The Bayesian analysis failed to converge after 45 days of computer time (standard deviation of split frequencies ~ 0.07). The resulting majority-rule consensus of post–burn-in trees placed *A. proboscis* in a large basal polytomy with other members of the Dactyloa clade (Etheridge, 1959; Guyer and Savage, 1986; Castañeda and de Queiroz, 2011) or *latifrons*-series (Etheridge, 1959) species. The parsimony results were better resolved, and we thus present these results to communicate a tentative hypothesis for the relationships of *A. proboscis*.

A part of the strict consensus of most parsimonious trees is shown in Figure 4. All relationships shown were present in fewer than 50% of bootstrap replicates. *Anolis proboscis* appears as a member of a clade of *Phenacosaurus*-group *Anolis*. These high-elevation South American species share large smooth headscales and short limbs and tail. Morphologically, they resemble twig-ecomorph *Anolis* of the Caribbean (Losos, 2009). We were unable to obtain specimens of the other proboscis anoles *A. laevis* and *A. phyllorhinus*, and future work will include these species in phylogenetic analyses. The external morphology of *A. laevis* (Williams, 1979) suggests it also is a member of the phenacosaur clade, but *A. phyllorhinus* appears more similar to *A. punctatus* (Rodriguez *et al.*, 2002), which was placed outside of the clade shown in Figure 4.

Concluding Comments. The recent rediscovery of *Anolis proboscis* and subsequent flood of information on it has offered a window into the life of a remarkable species, but much remains to be learned of *A. proboscis* and the other proboscis anoles. The Peruvian proboscis anole *A. laevis* awaits rediscovery, and the phylogenetic relationships of all proboscis anoles remain poorly known. The diurnal behavior of these species is only beginning to be understood, and the evolution of the proboscis (both within *Anolis* and in comparison with distantly related forms such as *Ceratophora tennenti*); its use in natural breeding, territorial displays in conjunction with or independent of the dewlap, or both; and its internal anatomy are

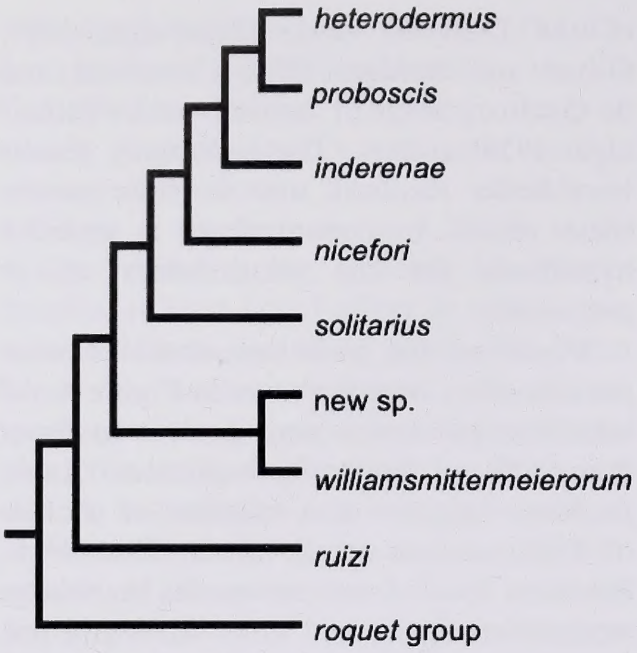

Figure 4. Estimated relationships of *Anolis proboscis* according to a strict consensus of optimal trees from parsimony analyses. Clade shown is nested within the basal alpha group of *Anolis* (i.e., Etheridge's [1959] *latifrons* series).

all fertile subjects for future research. We hope the present work helps to lay a foundation for the understanding of these cryptic and fantastic forms.

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